

SOCIAL LEARNING IN
NEOLAMPROLOGUS PULCHER
AN UNDERGRADUATE RESEARCH THESIS

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Abstract:

Animals can receive new information via social learning, and acquisition of social information in a changing environment can bestow benefits to an observer by reducing the costs of acquiring information. Many species live in hierarchal social groups in which individuals vary in status. Status may influence learning because dominant individuals are more noticeable and likely more successful at obtaining resources. However, it may also be more pertinent for an observer to obtain information from a similar ranked individual. Little is known about how social status influences learning, thus I performed an experiment to determine how the social status of a demonstrator influenced the use of social information in the highly social cichlid fish *Neolamprologus pulcher*. I presented social information about food location that conflicted with personal information. I tested two hypotheses. The first is that information obtained from dominant demonstrators would be more important; if so, I predicted that observers would spend more time on a demonstrator's side of the tank. Alternatively, I hypothesized that information obtained from similarly ranked demonstrators would be more important; if so, I predicted that observers would spend more time on a demonstrator's side of the tank. Dominant male observers were the most affected by the social status of the demonstrator, especially when the demonstrator was a dominant female and, thus, they spent more time on the dominant females' side of the tank compared to any other demonstrator type.

Introduction:

In a changing environment, biologically relevant information, such as location of food, areas safe from predators, and mates can quickly become outdated. Consequently,

individuals can gain reproductive and survival benefits by updating information about their environment (Boyd & Richerson 1985, Boyd & Richerson 1988, Kendal et al. 2009). The process by which an individual acquires new information and modifies its behavior accordingly is defined as learning (Kamil & Yoerg 1982). Learning can be broken down into two types: asocial learning and social learning. Asocial learning occurs when an individual learns through trial and error (Rendell et al. 2010). Conversely, social learning is defined as learning that is influenced by the observation or interaction with another organism, usually a conspecific (Box 1984).

The acquisition and exploitation of social information can bestow fitness benefits to an observer. That is, if an observer's personal information in regards to their current environment is outdated, it may be beneficial for them to follow the behavior of a demonstrator in order to save themselves the cost of learning a new behavior based on trial and error (Kendal et al. 2005). For example, if an observer watches another individual foraging for food, this may provide information that there is low predation risk. In this case, the observer does not have as much personal risk in order to sample the environment for predators (Brown & Laland 2003, Kelley et al. 2003).

While benefits exist to social learning, there are also costs. Individuals face a tradeoff between obtaining costly but accurate information from personal learning and socially-acquired information that is cheap and perhaps less reliable (Boyd & Richerson 1985). For example, theoretical models have demonstrated that observers that learn from social learning have higher fitness than asocial learners, but only when copying is rare in the population (Boyd & Richerson 1985, Rogers 1988, Giraldeau et al. 2002). As the frequency of social learning increases, the value of this strategy starts to decline because

fewer individuals are sampling the environment and the information that is being transmitted via social learning is more outdated and less reliable (Laland 2004).

Various social factors can influence social learning. For example, older individuals within a population are considered more influential because they have acquired patterns of behavior that have allowed them to avoid predation, find food, and reproduce successfully (Galef & Laland 2005). Possibly, then these individuals are a reliable source of information. In support of this note, individuals raised by older conspecifics experienced an increase in fitness benefits (Kempes et al. 2008, Arnold & Taborsky 2010, Taborsky et al. 2012).

The social status of the demonstrator can also affect how individuals use socially acquired information. Many species of animals live in hierarchal groups where dominant, high-ranking individuals are larger, stronger, and/or more aggressive and thus more apt to obtain resources (Broom et al. 2009). The presence of a dominant demonstrator may influence how an observer processes and chooses to use social information. Subordinate individuals may already be paying attention to dominant demonstrators in order to avoid aggression (Nicol & Pope 1994) and, by noticing them, the subordinate may also notice new information, such as the location of a food source or potential mates. Alternatively, it is possible that dominants may choose to pay attention to subordinates because, often times, subordinates are less neophobic and more willing to sample new environments (Boogert et al. 2006, Seok An et al. 2011, Krueger et al. 2014) which could lead to access to new resources. In this case, it is plausible that a dominants would weight information given from a subordinates. Additionally, a subordinate observer may greatly benefit from observing a dominant demonstrator because higher-ranking individuals have been

successful at obtaining resources, mates, etc. (Nicol & Pope 1994, Broom et al. 2009).

Though the observer may not improve upon its own status by copying a dominant demonstrator, it still may gain similar benefits by observing the dominant.

Support exists for the hypothesis that social dominance can be a significant factor in explaining individual variation in information use (Seok An et al. 2011). For example, a study found that, in adult laying hens (*Gallus gallus domesticus*), dominant demonstrators attracted more observers and that these observers used social information more than the other hens in the flock that had been exposed to socially subordinate or unfamiliar demonstrators (Nicol & Pope 1994). Domestic horses (*Equus caballus*) are also more likely to change their behavior after observing a more dominant individual following a human experimenter compared to if they observed a subordinate individual following a human experimenter (Krueger et al. 2008).

On the other hand, social information given by a demonstrator of similar rank as the observer might be a more accurate source of information because it more applicable to the observer. For example, in baboons, adults and juveniles forage separately and, because of this, they do not have the same feeding techniques (Cambefort 1981). In this example, it is better for a juvenile baboon to pay attention to another juvenile because this individual has the most relevant information about foraging compared to an adult, though this was not tested specifically in that study.

For my study, I used a cooperatively breeding cichlid (*Neolamprologus pulcher*) to determine if social status influenced the way in which an observer perceived and processed new information about the location of food. *N. pulcher* is native to Lake Tanganyika in East Africa and is widely known as being a cooperative breeding species,

with size-based social hierarchies (Fischer et al. 2015). *N. pulcher* lives in groups that are composed of a dominant pair and 0-20 subordinate helpers of both sexes (Wong & Balshine 2011). These characteristics make *N. pulcher* an excellent model system to study complex relationships between social structure and learning. Several investigators have conducted studies to determine how social status influences behavior this species. For example, a male breeder (who is typically the most dominant male in group) will threaten subordinate helpers with aggression, as well as the risk of expulsion (Dierkes et al. 1999, Skubic et al. 2004).

The goal of my experiment was to understand how social status influences learning in *N. pulcher*. I focused on two alternative hypotheses: (1) Information obtained from a dominant demonstrator is more important or more likely to be transmitted because the observer is either already paying attention to dominant individuals or the information is more useful. Thus, when observers are presented with social information that conflicts with their personal information, they will use the socially acquired information more when demonstrators are socially dominant to themselves and spend more time on those demonstrators' side of the tank (compared to demonstrators of a lower rank). (2) Information obtained from a similar ranked individual is more important or more likely to be transmitted because observers perceive those demonstrators' behavior as more applicable to its current environment. Thus, when observers are presented with social information that conflicts with their personal information, they will shift towards using the socially acquired information more when demonstrators are socially similar to themselves and spend more time on those demonstrators' side of the tank (compared to demonstrators of higher or lower rank).

Methods:

Study Species

All *N. pulcher* in this experiment were obtained from an aquarium fish wholesaler (Old World Exotic Fish, Homestead, FL, USA). I formed 16 groups of four individuals, a dominant male (DM), a dominant female (DF), a large subordinate male (LSM), and a small subordinate (SS). The SS were too small to sex and, thus, it was unknown whether SS individuals were male or female in this experiment. The standard length (defined as the length from the tip of the snout to the posterior end of the last vertebra) of each fish was measured and DM were found to be between 63-73 mm in length, while DF were between 48-72 mm, LSM were between 38-57 mm, and SS were between 27-40 mm. Though some overlap in length existed among groups, the DM was typically the largest individual within a home group, followed by the DF, LSM, and SS, respectively. Because of the limited number of fish available for use in my study, there were two instances where the DF was the same size or larger than the DM in her group.

For my experiment, I focused on information use by DM, DF, and SS as my observer fish who were presented with social information, but LSMs were still used as stimulus fish to provide social information. A concurrent experiment explored use of social and personal information by LSM (Hoskins, personal communication). In the case of mortality, groups that had less than three fish were excluded from being observer fish, but they were still used as stimulus fish if their neighbors were still being tested.

Housing conditions

Groups were housed in 114 L aquariums filled with sand substrate with an average depth of 25 mm. Each tank included two halves of a clay flowerpot to serve as a shelter and breeding substrate. Tanks were equipped with two PVC tubes (5 cm) suspended near the surface of the water on each side of the tank to serve as refuges for any fish receiving aggression. Tanks were also equipped with a slate (9.8 x 9.8 cm) that was placed in the sand on the left side to serve as a landmark so fish could differentiate between the two sides of the tank. Opaque barriers were placed between every other tank, which allowed for each group to only have one visible neighboring group to interact with. All tanks were maintained on a 12:12 hr light:dark cycle and under conditions reflecting those in Lake Tanganyika (temperature = 23-28 °C, pH = 7.8-8.4). Every two weeks, levels of pH, ammonia, nitrate, and nitrite were checked in each home tank. During this time, tanks were also cleaned of algae and a 25% water change was performed.

Tank Set-Up

Prior to release, all fish were measured, weighed, sexed, and individually marked via elastomer injection. Dominant males and small subordinates each received dorsal fin clips to help identify them throughout the experiment. To assemble groups, LSM and SS were released one day before the DM and DF, during which time the dominants were maintained in net cages in the tank into which they would eventually be released. During the first few days of the experiment, I observed each group frequently for any indications of aggression and eviction of group members. In these instances, either the individual receiving the aggression or the one that was being the aggressor was isolated. This

procedure has been used to assemble groups in other studies of this system (e.g., Hamilton & Ligocki 2012). I waited 28 days before testing to allow groups and neighbors to be established.

Beginning twenty-one days following release of all group members (7 days before starting the experiment), fish were trained to associate one side of the tank with food. Within each neighboring pair of tanks, the fish in one tank were trained to feed on the left, whereas the fish in the other tank were trained to feed on the right (Figure 1a). The fish were fed one to three times each day, every day throughout the entirety of the experiment. A small amount of frozen food (bloodworms, brine shrimp, and/or daphnia) was delivered to the fish in the front corner on the designated side for each tank, and this is how all fish were fed throughout the entire experiment. It should be noted that all fish in the tank were fed together. This was done so that individuals could learn about food location via their own exploration or through social learning. Thus, personal information in this experiment is not necessarily asocially acquired. Also, by not netting and isolating the fish to feed them, stress caused by handling was avoided.

Food Association Test

After the first 7 days of feeding in one location, food association tests were done to determine whether the fish had learned to associate one side of the tank with food prior to providing conflicting social information. All trials were conducted in an experimental tank that was identical to home tanks, except that there were no clay pots for fish to use as shelters (Figure 1b). During a food association test, the focal fish was first placed in a transparent tube (10.16 cm in diameter) in the center of a testing tank and allowed 2

minutes for habituation. Afterwards, a small amount of food was deposited on each side of the tank and the focal fish was released from the tube and allowed to swim freely around the tank. The amount of time the focal fish spent on each side of the tank was timed for 10 minutes (standardized trial time). Changing sides was defined as when half of the fish's body had moved to the other side of the tank.

The number of bites (of food) the focal fish consumed was recorded, as was any unusual behavior (hiding in PVC tubes or behind the filter/heater, not moving, etc.) that was exhibited. When the trial was over, the focal fish was placed back into its respective home tank and observed to see if they experienced any stress. If they spent at least six out of 10 minutes on the side that they were trained to associate with food, I considered that the focal fish had learned the association between food and location. If the focal fish successfully made the association, it moved on to a social test the following day. If it failed, I waited at least 4 days before testing it again to see if it associated the correct side with food. In the interim, all fish continued to be fed on the same side of the tank that they were being tested on. If an individual failed 9 food association trials in a row, it was removed from the experiment altogether because, by this point, the fish had been in the experiment for at least 30 days and it was assumed that they had not learned proper association and would not learn it through further testing.

Social Test

Once a fish passed a food association test, they moved onto a social test the following day. During a social test, the observer was first placed in a transparent tube in the center of the testing tank and allowed 2 minutes for habituation (Figure 1c). Next, a

capped tube (10.16 cm in diameter) was filled with aquarium water and a demonstrator fish was placed inside of it. The tube with the demonstrator was then placed on the opposite side of the tank that the observer learned to associate with food. The demonstrator was then allowed 2 minutes for habituation. In a social test, there were three possible stimulus presentations. In a “food” trial, the demonstrator was fed a small amount of food and allowed 2-3 minutes to feed. In a “no food” trial, the demonstrator was not fed, but allowed 2-3 minutes were allowed to pass. This was done to see if there was an attraction/repulsion to/from the demonstrator that may vary among social statuses of demonstrators and observers. In a “no fish” control trial, an empty capped tube (with no demonstrator fish) was placed on its assigned side and remained there for 3 minutes. For all treatments, the stimulus then was removed and one minute was allowed to pass.

Next, a small amount of food was delivered to each side of the tank and the observer was released and allowed to swim freely around the tank. The amount of time the observer fish spent on each side of the tank, as defined above, was timed for 10 minutes. The number of bites (of food) the observer fish consumed was recorded, as was any unusual behavior (hiding in PVC tubes or behind the filter/heater, not moving, etc.) that was exhibited. When the trial was over, the observer and demonstrator (if there was one) fish were placed back into their respective home tanks and observed to see if they experienced any stress. At the end of each testing day a 50% water change was performed on the experimental tank.

After at least 4 days of retraining, observer fish went through another side test to determine if they still associated the side on which they were trained with food. If they passed using the same criterion as before (6/10 minutes), they moved on to another social

test that included a different demonstrator/stimulus. This was repeated until observer fish completed all 9 social tests or until they failed out of the experiment. Trials for all three statuses (DF, SS, and DM) were randomized to avoid any testing bias. Tests were conducted between the hours of 0800 and 2000 from 12 May-16 October 2016. Trials were conducted by six different people all of whom followed the same procedural protocol that was approved by The Ohio State University Institutional Animal Care and Use Committee (Protocol 2008A0095).

Data Analysis

All analyses were conducted using SPSS 24 with significance levels set to $\alpha=0.05$. To determine what extent observers of each status (DM, DF, and SS) changed the side that they fed on based on the presence of another individual, I compared the proportion of time spent on the untrained side (the side with the demonstrator) between the “no food” control for each demonstrator status (four tests total) and the “no fish” control using a Friedman test. If I found a significant effect, I conducted a series of post-hoc Wilcoxon signed rank tests to compare the “no food” and “no fish” trials for each demonstrator status.

To determine if providing food changed the side that observers fed on, I compared the “food” and “no food” trials by running Wilcoxon signed rank tests comparing proportions of time spent on the untrained side between “no food” and “food” trials for each demonstrator status. Finally, to determine if the observers changed the side that they fed on based on the social rank of the demonstrator, I ran Friedman and Kruskal-Wallis tests. The Friedman test was used to determine the effect of status of the demonstrator on

the differences in time spent on the demonstrators' side between the "food" and "no food" trials for each observer status. The Kruskal-Wallis was used to test the effect of observer status on the difference in time spent on the demonstrators' side between "food" and "no food" trials, for each type of demonstrator.

Results:

Comparison between "no food" and "no fish" trials

These tests were run to determine what extent observers changed their behavior when another individual was present. In comparison between "no food" controls and "no fish" controls, only DM observers showed a significant effect of the presence of another individual (Friedman test, $n=5$, $P=0.038$; Figure 2a), while DF (Friedman test, $n=5$, $P=0.721$, Figure 2b) and SS (Friedman test, $n=5$, $P=0.647$, Figure 2c) did not. DM observers spent more time on a DF demonstrator's side when she had not been fed during a "no food" trial than when she had been presented with a "no fish" control trial, though the results were not statistically significant (Wilcoxon signed rank test, $Z=-1.690$, $P=0.091$; Figure 2d). The presence of a DM (Wilcoxon signed rank test, $Z=-0.135$, $P=0.983$), LSM (Wilcoxon signed rank test, $Z=-1.521$, $P=0.128$), and SS ($Z=-0.845$, $P=0.398$) demonstrators also did not have a significant effect on DM observers relative to the "no fish" control.

Comparison between "food" and "no food" trials

These tests were run to determine if there was a transfer of information about the location of food. DM observers tended to spend more time on the DF demonstrator's side

of the tank during a “no food” trial compared to “food” trial, and these results were statistically significant (Wilcoxon signed rank test, $Z=-2.201$, $P=0.028$; Figure 3a). There was also a tendency for DM observers to spend more time on a DM demonstrator’s side of the tank during a “food” trial compared to a “no food” trial, though these results were not statistically significant (Wilcoxon signed rank test, $Z=-1.872$, $P=0.075$; Figure 3b). No significant difference was found between the proportion of time spent on the demonstrator’s side of the tank compared to the learned side of the tank when the demonstrator was a LSM or SS. I did not find a significant effect on the amount of time a DF observer spent on the demonstrator’s side of the tank during a “food” trial compared to a “no food” trial, regardless of demonstrator type (DM demonstrator: Wilcoxon signed rank test, $Z=-1.363$, $p=0.173$; DF demonstrator: Wilcoxon signed rank tests, $Z=-0.420$, $P=0.674$; LSM demonstrator: Wilcoxon signed rank test, $Z=-0.105$, $P=0.917$; SS demonstrator: Wilcoxon signed rank test, $Z=-1.183$, $P=0.237$) There was a tendency for SS observers to spend more time on the DF demonstrator’s side of the tank during a “food” trial compared to during a “no food” trial, though the results were not statistically significant (Wilcoxon signed rank test, $Z=-1.690$, $P=0.091$; Figure 3c) and no other demonstrator had a significant effect on the time SS observers spent on the demonstrator’s side of the tank (DM demonstrator: Wilcoxon signed rank test, $Z=-0.105$, $P=0.917$; DF demonstrator: Wilcoxon signed rank test, $Z=-1.690$, $P=0.091$; LSM demonstrator: Wilcoxon signed rank test, $Z=-0.700$, $P=0.484$; SS demonstrator: Wilcoxon signed rank test, $Z=-1.540$, $P=0.123$).

Effect of demonstrator status on behavior

These tests were run to determine if observers changed their behavior based on the status of the demonstrator that was feeding. Only DM observers were affected by the social status of the demonstrator (Friedman test, $n=5$, $P=0.014$; Figure 4a), whereas DF (Friedman test, $n=4$, $P=0.682$, Figure 4b) and SS (Friedman test, $n=4$, $P=0.440$, Figure 4c) observers were not. Only DF demonstrators had a significant effect on the behavior of the observers (Kruskal-Wallis test, $H=9.462$, $P=0.009$, Figure 4d), while DM (Kruskal-Wallis test, $H=2.889$, $P=0.236$), LSM (Kruskal-Wallis test, $H=0.932$, $P=0.628$), and SS (Kruskal-Wallis test, $H=0.808$, $P=0.668$) did not.

Discussion:

Previous studies have shown that the social rank of a demonstrator can influence learning in various species (Nicol & Pope 1994, Nicol & Pope 1998, Pongrácz et al. 2006, Krueger et al. 2008). In this experiment, I found that dominant males were the most influenced by the presence of a demonstrator, particularly when the demonstrator was a dominant female. This lends support to my first hypothesis that individuals place more emphasis on dominant demonstrators. Dominant females are similar in size and dominance to dominant males so it is reasonable to believe that the dominant males prioritized information given by dominant females.

When comparing the proportion of time that dominant males spent on dominant females' side of the tank during a "food" trial and "no food" trials, they overall spent less time on their side when they had been fed. This species is not known to defend feeding patches in the wild, but other cichlid species can be induced to defend feeding patches in

a laboratory setting (Barlow 1993, Hamilton 2004) so it is possible that dominant males may have avoided the dominant females' side after they had been fed because they were avoiding aggressive competition over resources (Lindstedt & Hamilton 2013).

Alternatively, dominant males may not have been interested in interacting with dominant females as potential mates, if they were already focusing on another activity.

When the demonstrator was a dominant male, dominant male observers tended to spend more time on the demonstrator's side of the tank during a "food" trial compared to a "no food" trial, though the results were not significant ($P=0.075$). Dominant male demonstrators are the most similar to dominant male observers and these results may also be consistent with the second hypothesis that individuals place more emphasis on more similar/lower ranked demonstrators; but, as of yet, they are inconclusive. In dogs (*Canis familiaris*), dominant individuals tend to focus on dominant humans and they will preferentially learn from a human demonstrator rather than from another dog (Pongrácz et al. 2008). It is possible that this is the case in *N. pulcher* and that dominant males tend to prioritize information from other dominants simply because they prefer to use information provided by the highest ranking individual within the group. The fact that dominant males did not increase the amount of time spent on the demonstrator's side of the tank when the demonstrators were large subordinates or small subordinates also supports the first hypothesis. Older and more dominant individuals tend to avoid the costs of acquiring potentially disadvantageous feeding behaviors from younger and more subordinate demonstrators (Brown & Laland 2003).

Dominant females paid no particular attention to the social status of a demonstrator in this experiment (Figure 4b). This may be due to the fact that they were

paying more attention to their own environment compared to the environment of the demonstrator (who was their neighbor). Additionally, the dominant females might have higher stress levels compared to other ranks throughout the testing procedure and this may have disrupted their performance. A social learning study on starlings (*Sturnus vulgaris*) found that constant removal of dominant individuals from the group might have created chronic social pressure that carried over into the individual testing situation and created a negative impact, though it should be noted that these results were found in dominant males (Boogert et al. 2006). Dominant females in *N. pulcher* are found to be similar to dominant males in that they exhibit similar dominance behavior, testosterone levels, and AVT gene expression (involved in regulation of dominant and aggressive behavior in cichlids) compared to small subordinates (Aubin-Horth et al. 2007). Thus, it is possible that dominant females perceived themselves to be at the top of the dominance hierarchy and, therefore, did not need to pay attention to others because it would not have been applicable to them.

Social learners are often younger and lower in the dominance hierarchy than are non-social learners (Krueger et al. 2014). However, in this experiment, data obtained from small subordinate observers did not support either hypothesis explicitly. When comparing the small subordinates' response to food when the dominant female was the demonstrator, they tended to spend more time on the females' side after a "food" trial compared to a "no food" trial, though the results were not significant ($P=0.091$). The small subordinates may have been able to perceive that there was new information about location of food, but their motivation level may not have been high because they were also using that information to avoid conflict with the dominant females. For example, a

study on chimpanzees (*Pan troglodytes*) revealed that the proximity of a dominant individual inhibited subordinates from performing food acquisition tasks because they had previously learned that the dominant individual would steal their reward (Chalmeau & Gallo 1993).

As far as I know, my experiment is the first to determine how social status influences learning in *Neolamprologus pulcher*. I found only limited support that the social status of a demonstrator affects the transmission of information learning because only dominant males were affected and only when the demonstrator was a dominant female. Future studies should focus on repeating this experiment with a larger sample size in order to obtain stronger results as it is likely that these fish are capable of learning and that sociality can play a part in the process.

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Figures:

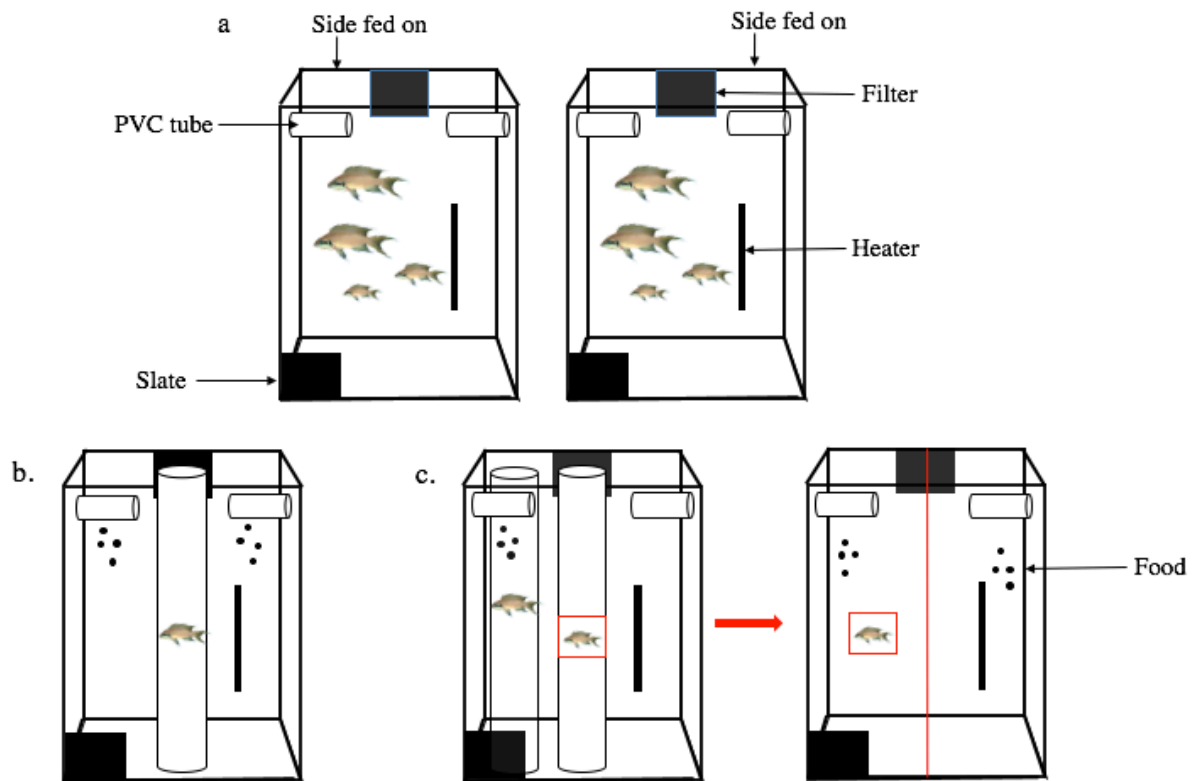


Figure 1. a. Example of neighboring tanks. **b.** Habituation phase in the food-association test. **c.** Presentation of social information about the location of food that conflicts with private information. In this example, the focal fish had been trained to feed on the right side of the tank.

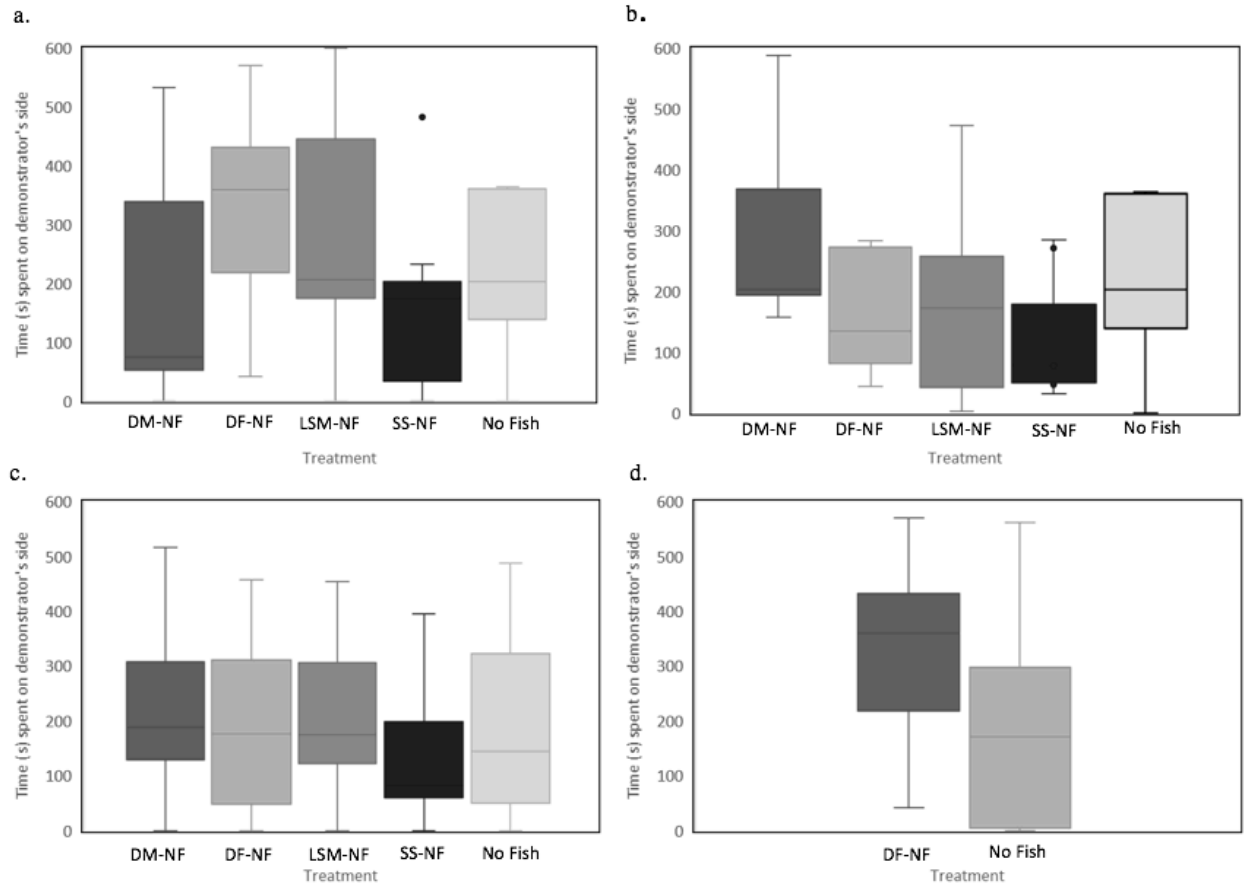


Figure 2. Boxplots show the minimum and maximum amount of time (whiskers), as well as the median amount of time (median line) that observers spent on the demonstrator's side. Boxplots also show the interquartile range, which represents how much time half of the observers spent on the demonstrator's side. Outliers are plotted as individual points and are defined as being 3 times the interquartile range **a.** Effect of demonstrator on DM observers. Dominant males were significantly affected by the presence of a demonstrator, $P=0.038^*$. **b.** Effect of demonstrator on DF observer. Dominant females were not significantly affected by the presence of a demonstrator, $P=0.721$. **c.** Effect of demonstrator on SS observers. Small subordinates were not significantly affected by the presence of a demonstrator. $P=0.647$. **d.** Effect of control trials on DM observers. Dominant males spent more time the dominant females' side when they had not been than in the "no fish" control trials. $P=0.091$.

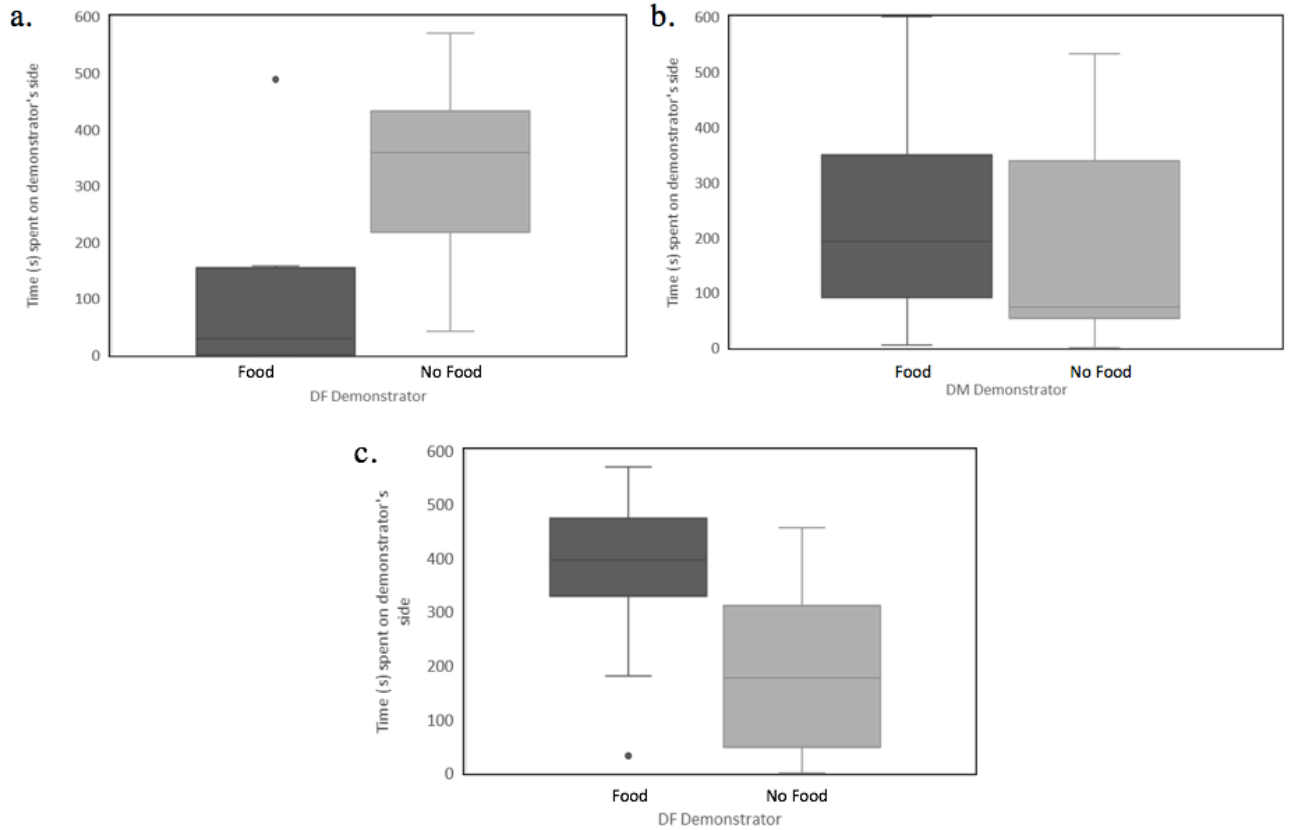


Figure 3. Boxplots show the minimum and maximum amount of time (whiskers), as well as the median amount of time (median line) that observers spent on the demonstrator's side. Boxplots also show the interquartile range, which represents how much time half of the observers spent on the demonstrator's side. Outliers are plotted as individual points and are defined as being 3 times the interquartile range. **a.** Effect of food information on DM observer when demonstrator is DF. Dominant males spent significantly more time on the demonstrator's side of the tank when the dominant female had not been fed compared to when she had been fed, $P=0.028^*$. **b.** Effect of food information on DM observer when demonstrator is DM. Dominant males spent more time on the dominant males' side of the tank when they had been fed compared to when they had not been fed, $P=0.075$. **c.** Effect of food information on SS observer when demonstrator is DF. Small subordinates spent more time on dominant females' side of the tank when they had been fed compared to when they had not been fed, $P=0.091$.

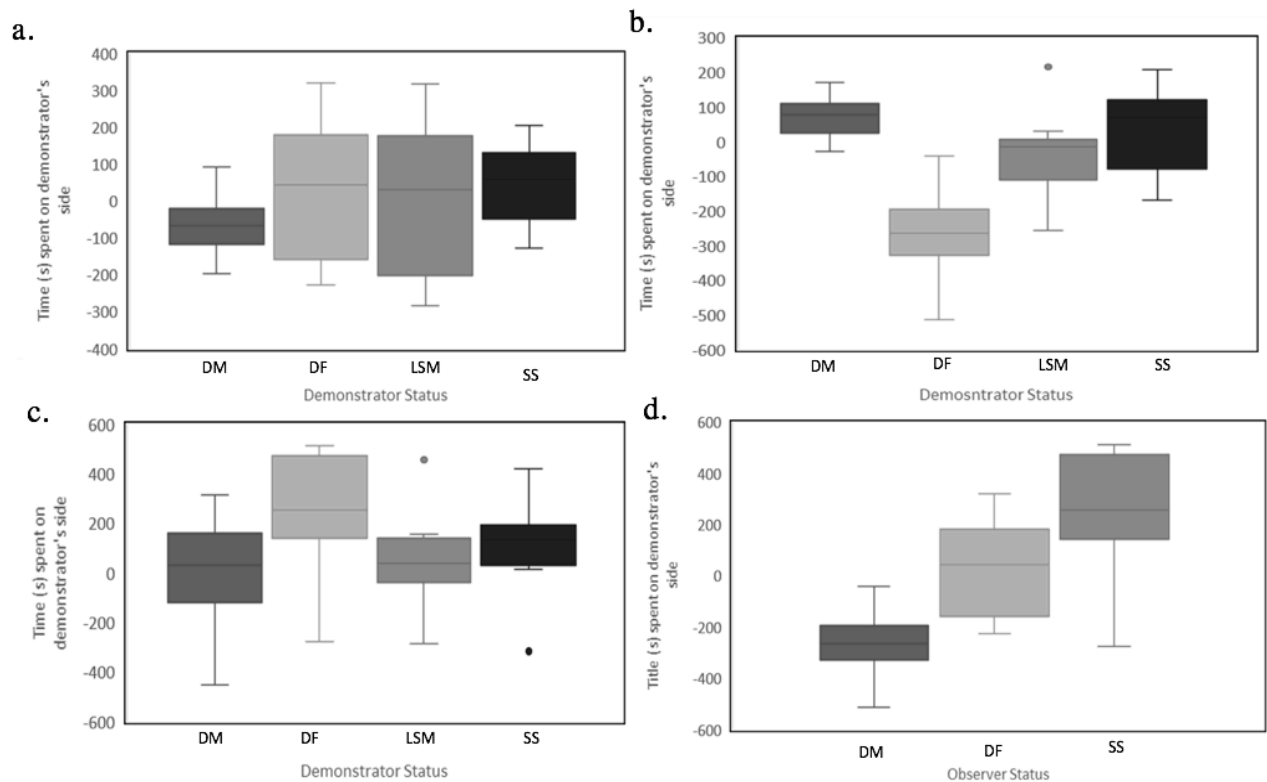


Figure 4. Boxplots show the minimum and maximum amount of time (whiskers), as well as the median amount of time (median line) that observers spent on the demonstrator's side. Boxplots also show the interquartile range, which represents how much time half of the observers spent on the demonstrator's side. Outliers are plotted as individual points and are defined as being 3 times the interquartile range. **a.** Effect of demonstrator social status on DF observer. Dominant male observers were the most affected by the social status of demonstrator, $P=0.014^*$. **b.** Effect of demonstrator social status on DM observer. Dominant female observers were not affected by social status of demonstrator, $P=0.682$. **c.** Effect of demonstrator social status on SS observer. Small subordinate observers were not affected by social status of demonstrator, $P=0.440$. **d.** Effect of DF demonstrator on observers. Dominant female demonstrators had the most effect on observers, $P=0.009^*$.